Received: 3 May 2024 | Revised: 20 August 2024 | Accepted: 21 August 2024
DOI: 10.1111/gcb.17494

Global Change Biology WILEY

RESEARCH ARTICLE

Water restriction alters seed bank traits and ecology in Atlantic Forest seasonal forests under climate change

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Funding information
Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brazil (CAPES); Fundação de Amparo à Pesquisa e Inovação do Espírito Santo (FAPES); National Council for Scientific and Technological Development (CNPq, Programa de Capacitação Institucional—PCI/INMA) of the Brazilian Ministry of Science, Technology and Innovation (MCTI)

Abstract

The soil seed bank (SSB) is one of the key mechanisms that ensure the perpetuity of forests, but how will it behave in the scenarios projected for the future climate? Faced with this main question, still little explored in seasonal tropical forests, this study evaluated the germination, ecological attributes, and functional traits of the SSB in a seasonal forest in the Atlantic Forest. Forty-eight composite samples of the SSB were collected from 12 plots, distributed across four treatments, each with 12 replicates. The samples were placed in two climate-controlled greenhouses, establishing two environments of controlled climatic conditions, both with two levels of water, as follows: Cur: current scenario without water restriction; Cur_WR: current scenario with water restriction; RCP8.5: future scenario without water restriction; RCP8.5_WR: future scenario with water restriction. The germinants were identified, and their ecological attributes and functional traits were obtained. Leaf area and biomass production, differences in abundance, richness, and diversity were evaluated, along with analysis of variance to assess the interaction between water levels and scenarios. All ecological attributes and functional traits evaluated drastically decreased in the future projection with water restriction, with this restriction being the main component influencing this response. The increased temperature in the future scenario significantly raised water consumption compared to the current scenario. However, persistent water restrictions in the future could undermine the resilience of seasonal forests, hindering seed germination in the soil. Richness and abundance were also adversely affected by water scarcity in the future scenario, revealing a low tolerance to the projected prolonged drought. These changes found in the results could alter the overall structure of seasonal forests in the future, as well as result in the loss of the regeneration potential of the SSB due to decreased seed viability and increased seedling mortality.

KEYWORDS
Atlantic Forest, biomass productivity, climate crisis, CO_2 increase, ecosystem resilience, mitigation actions, seedling emergence

1 | INTRODUCTION

Drought causes a diverse and complex set of changes in tropical forest ecosystems (Bonal et al., 2016), which condition remnants to react in different ways to climate changes (Boucher et al., 2020). For instance, drought negatively impacts forest productivity and alters plant chemical defenses, leading to increased herbivory activity (Hamann et al., 2021). In this sense, species' response to climate change can vary from extinction to resilience (Moritz & Agudo, 2013). Therefore, understanding the relationship between drought, climate change, and their consequences on forest remnants is essential for developing effective conservation strategies that consider both the mitigation of impacts and the adaptation of species and ecosystems to new climatic conditions.

Soil seed banks (SSBs) are important reservoirs of species biodiversity and ensure the resilience of forests, as well as being vital in shaping the composition and structure of these remnants in the future (Gioria et al., 2020; Vandvik et al., 2016; Yang et al., 2021). They function as a natural recovery mechanism, allowing forests to regenerate after disturbances and ensuring the continuity of these ecosystems over time (Yang et al., 2021). However, germination marks a critical transition in plant life, prone to high mortality, as seedling climatic niches are narrower compared to adult trees (Bell et al., 2014; Dobrowski et al., 2015), making seeds and seedlings more vulnerable to disturbances (Boucher et al., 2020; Ma et al., 2020). Thus, strong selective pressure is expected on seedlings to accurately adjust them to the imposed environmental conditions (Metz et al., 2018).

The resilience of the SSB depends on understanding how climate change will influence seed emergency (Gioria et al., 2022). With the increase in atmospheric CO_2 concentration, conditions predicted in future scenarios, such as changes in temperature, water availability, and fire frequency in natural habitats, can affect seed dormancy, production, and persistence, causing changes in the timing of germination, growth, and seedling survival (Boucher et al., 2020; IPCC, 2014; Jiménez-Alfaro et al., 2016; Long et al., 2015; Ooi, 2012; Walck et al., 2011; Zou et al., 2021). Because of these changes, soil temperature and moisture also alter. The temperature rises in open environments and/or with sparse vegetation, especially in arid vegetation and seasonal forests, which can accelerate the decline in seed viability, compromise species' ecological strategies, and negatively affect species richness while positively impacting seedling mortality (Ooi, 2012; Ooi et al., 2009; Silva, Calvi, et al., 2021). Thus, understanding the resilience of seed banks to climate change can provide more accurate predictions of the future distribution and survival of seasonal forests, but the response of seed banks and their persistence to the climate crisis is still poorly understood (Du et al., 2023; Ibáñez et al., 2007; Ma et al., 2020; Ooi, 2012; Panetta et al., 2018; Walck et al., 2011).

Given the above, the importance of studies on the resilience of seeds and seedlings becomes evident, concerning their emergency and growth behavior in response to environmental changes, thereby enhancing our ability to more effectively predict the impacts of the climate crisis, and providing new insights for conservation efforts, particularly in seasonal forest ecosystems. Thus, this study aimed to assess the emergency and floristic composition of the SSB under different climatic conditions in a seasonal forest in the biodiversity hotspot of the Atlantic Forest. To this end, the following hypotheses were tested: (i) The floristic composition and species abundance will be altered by global climate change; (ii) the studied scenarios will present low floristic similarity between each other; and (iii) functional traits will undergo modifications due to climate change.

2 | MATERIALS AND METHODS

2.1 | Study area

The SSB for this study was collected in the Pacotuba National Forest, a protected area located in the municipality of Cachoeiro de Itapemirim, Southern Espírito Santo state (20°44′43″ S and 41°17′29″ W) in southeastern Brazil (Figure 1). Covering an area of 450 ha and with an altitude of 100 m, it is considered a vegetation of great importance for the Atlantic Forest of Espírito Santo (Abreu et al., 2013), especially along the Itapemirim River basin. It is also one of the largest remnants of the semideciduous seasonal forest in the state, a phytophysiognomy that has been heavily devastated (ICMBio, 2011).

The Köppen climate classification for the region is Cwa, characterized by uneven rainfall throughout the year, with a rainy summer and a dry winter (Alvares et al., 2013). November and December have the highest rainfall, while August records the lowest, with an average annual precipitation of 1200 mm (Alvares et al., 2013; Incaper, 2019). Under these climatic conditions, the studied vegetation is classified as submontane semideciduous seasonal forest (Abreu et al., 2013), with the leaf seasonality of dominant tree species occurring during the dry winter. Additionally, the region features extensive flat areas with sparse and gentle elevations, as well as rocky outcrops at various points. The soil in the region is predominantly classified as Dystrophic Red-Yellow Latosol (LVAd) (Abreu et al., 2013).

2.2 | Data sampling

The collection of the SSB was carried out in June 2021, in 12 plots of 40 m × 50 m, previously defined by Abreu et al. (2013). The surface layer of soil (first 8 cm) was collected within each sampling unit, using a wooden frame ($25\,cm \times 25\,cm \times 8\,cm = 0.005\,m^3$) (Braga et al., 2008; Kunz & Martins, 2016). Three simple samples were collected per plot and then homogenized to form one composite sample per plot, which was then divided to cover the four different treatments (Figure 2) (Carmo et al., 2012).

The material was placed in hermetically sealed plastic bags labelled according to the plot and later arranged in perforated plastic trays with dimensions of 43.5 cm × 29.6 cm × 7.5 cm. These trays were then randomly placed under ceramic tiles

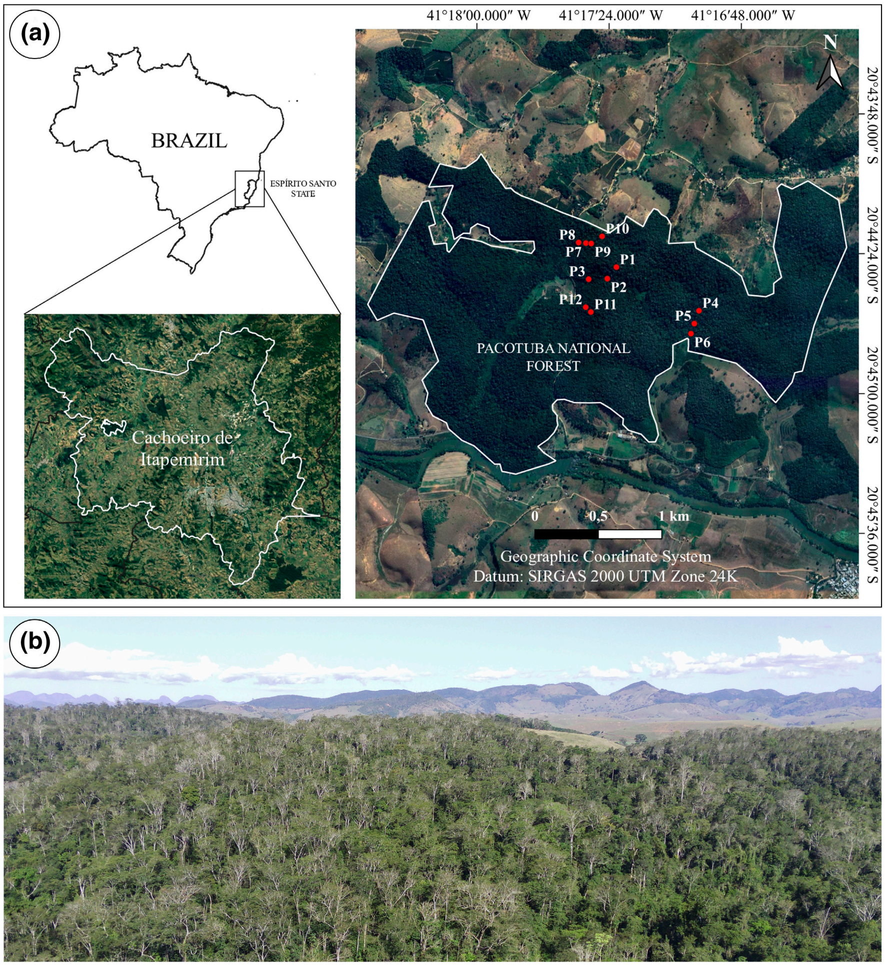

FIGURE 1 Location of Pacotuba National Forest, Cachoeiro de Itapemirim, Espírito Santo, Brazil, where (a) P1–P12 are the sampling units distributed in the vegetation, and (b) an overview of the local vegetation of the semideciduous seasonal forest. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

measuring 58 cm × 33 cm × 0.8 cm, distributed on metal benches in two greenhouses (Van der Hoeven®), with automated environmental control, in the experimental area of the Forest Meteorology and Eco-physiology Laboratory, Federal University of Espírito Santo—Jerônimo Monteiro (20°47′25″ S, 41°23′48″ W), to induce seed emergency and growth. The use of ceramic tiles allowed the trays to be moved without compromising the soil structure (Figure 2).

Two greenhouses were used (one scenario per greenhouse), each containing 24 trays of SSB distributed across four treatments: Cur (current scenario without water restriction), Cur_WR (current scenario with water restriction), RCP8.5 (future scenario without water restriction), and RCP8.5_WR (future scenario with water restriction) (Figure 2). Within each scenario, a completely randomized design was adopted, with the levels of water availability and different climatic scenarios as treatments.

In each treatment, four Type T thermocouple sensors were installed to measure soil temperature at a depth of 2 cm. The sensors were connected to a multiplexer, which was logged to a datalogger (Campbell Scientific Inc., CR-1000) powered by a 10 W solar panel. The datalogger was programmed to collect data every 10 s and record the average every 5 min.

Hourly surface soil temperature throughout the day was obtained at the beginning of the experiment using thermal images captured with a FLIR T430sc thermal camera (FLIR Systems, Wilsonville, OR, USA), with a resolution of 320 × 240 pixels. The distance between the camera and the trays was set at 0.4 m, and the emissivity used was 0.96. The images were processed using FLIR tools software.

To simulate the solar radiation reaching the forest interior, as measured in the understory of the remnant, the benches were prepared to reduce solar radiation, using shade cloth (50% shade). To control contamination from external diaspores, control trays with sterilized sand were randomly allocated on the benches. The assessment of the SSB was conducted from June 14 to November 13, 2021, totaling 5 months (155 days) of emergence.

2.3 | Definition of climate scenarios

To assess the impact of climate change on the SSB, two distinct scenarios were used: the current scenario (Cur) and the future scenario (RCP8.5). The first was represented by the current climate of the Pacotuba National Forest. Climate data for this scenario were established using the climatic normals from the nearest weather station to the remnant provided by the National Institute of Meteorology (INMET), located in the district of Rive, municipality of Alegre, Espírito Santo, Brazil. The mean, minimum, and maximum values of temperature and relative humidity were obtained to construct the

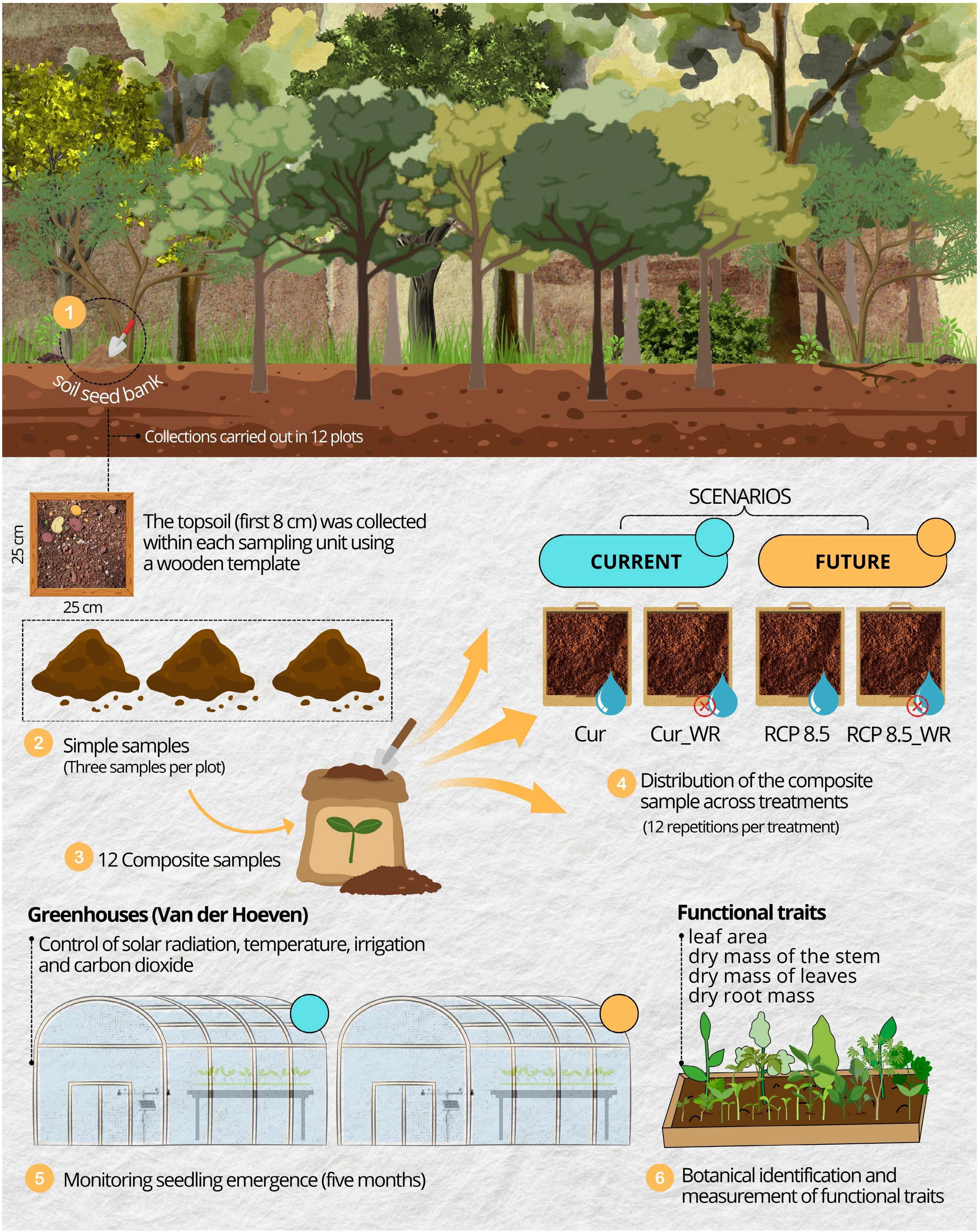

FIGURE 2 Flowchart of methodological steps for data sampling, treatment arrangement in greenhouses, and functional trait measurement.

temperature and vapor pressure deficit (VPD) curves throughout the day inside the greenhouse (Figure 3a,b).

The maintenance of microclimate conditions inside the greenhouses of this scenario was controlled by the pad cooling system, air-conditioning, heaters, and misting system for air humidification, which were activated by temperature controllers (Full Gauge®, MT-543Ri plus) and humidity controllers (Full Gauge®, AHC-80 plus).

The second scenario (future) was based on the projection of climate change from the representative concentration pathways 8.5 (RCP8.5) for the period 2081–2100, described in the fifth report (AR5) of the Intergovernmental Panel on Climate Change (IPCC, 2013). The projections were extracted from the environmental data platform of the Institute of Climatic Studies of Espírito Santo, which uses the Climate Change Projections for South America regionalized by the Eta model (PRO-JETA), from CPTEC, and the global HadGEM2-ES model, with a spatial resolution of 5 km. The grid points were based on the location of Jerônimo Monteiro—ES. In this scenario, the temperature and VPD variation curves were obtained by adding the values from the projection of the future climate scenario to the values from the climatic normals of the nearest weather station to the remnant (Figure 3a,b).

The characterization of the microclimate of the different scenarios was conducted using automatic weather stations installed inside the greenhouses (Table 1). The stations consisted of temperature and relative humidity sensors model CS500 (Campbell Scientific, Inc., Logan, UT, USA). Data were stored in a CR-10x datalogger (Campbell

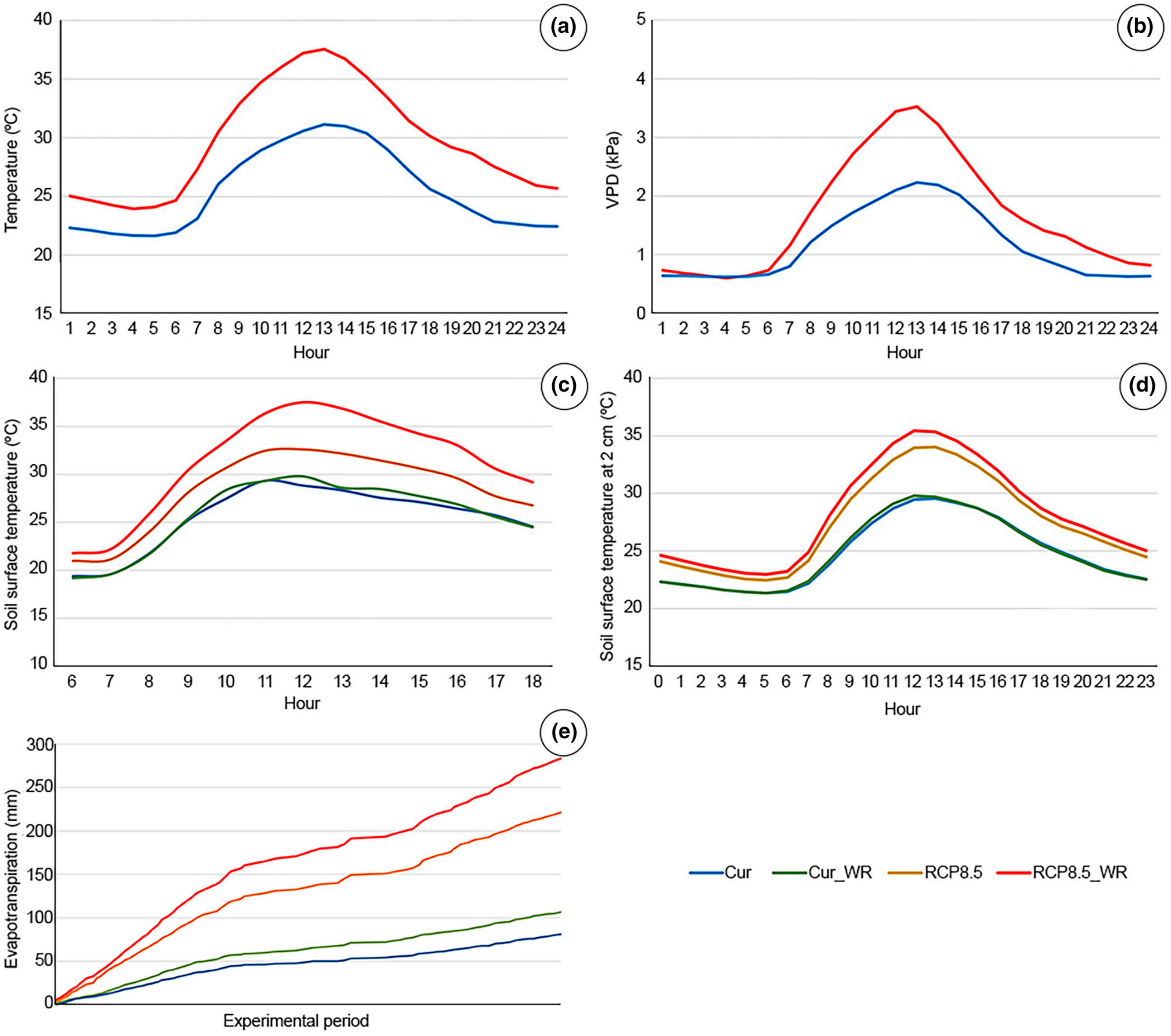

FIGURE 3 Hourly variation of mean air temperature (a) and vapor pressure deficit (b) during the experimental period (June 14, 2021 to November 13, 2021) for the current (Cur) and future (RCP8.5) scenarios inside the climate-controlled greenhouse. Hourly average throughout the entire experimental period of soil surface temperature (c) from 6 a.m. to 6 p.m., soil temperature at 2 cm depth (d) and total water consumption (evapotranspiration) (e) accumulated during the entire experimental period of the soil seed bank of the semideciduous seasonal forest remnant, Pacotuba National Forest, ES, Brazil.

TABLE 1 Microclimatic characterization of the simulated scenarios in the climate-controlled greenhouses, from June 14, 2021 to November 13, 2021, for the current (Cur) and future (RCP8.5) scenarios. Where RH, relative humidity, *T*, air temperature, and VPD, vapor pressure deficit (minimum, mean, and maximum values).

Climatic variables	Cur	RCP8.5
	Air temperature (°C)	
T_{min}	21.3	23.6
T_{mean}	25.5	29.7
T_{max}	31.7	38.4
	Air relative humidity (%)	
RH_{min}	49.0	44.1
RH_{mean}	67.1	64.9
RH_{max}	79.7	81.4
	Air VPD (kPa)	
VPD_{min}	0.5	0.6
VPD_{mean}	1.1	1.8
VPD_{max}	2.3	3.8

Scientific, Inc.), with readings taken every 10s and the storage of average values every 5min. The VPD was obtained through the difference between the saturation vapor pressure (es) and the partial vapor pressure (ea). The "es" was calculated using the Tetens equation (Pereira et al., 2002), and "ea" by the product of relative humidity and es. Climate change projections for the RCP8.5 scenario show an increase in temperature average of 4.2°C for the study region (Figure 3a,b).

The temperature and relative humidity variation programming of the control systems was monitored using Sistrad® software. To maintain the desired environmental conditions in each greenhouse of the study, the temperature control system was adjusted every 30min during the daytime and every hour during the nighttime. A fixed value was programmed for the desired humidity.

The injection system, which was activated daily from 8a.m. to 5p.m. in the future scenario. Monitoring of CO_2 concentration and possible adjustments within each greenhouse were conducted every day at 8a.m. and 12p.m. using a portable CO_2 analyzer (Testo AG, model testo 535). In this study, the average CO_2 concentration values for the scenarios were adjusted to 400ppm for Cur and 800ppm for RCP8.5.

2.4 | Water levels

The IPCC (2013) also predicts changes in precipitation and soil moisture. Therefore, in each scenario, two irrigation levels were maintained: irrigated trays (considered as control: non-stressed) and trays with 50% of the maximum soil water-holding capacity, to assess the seed bank's tolerance to water stress. Control of water availability levels was performed using the gravimetric method (weighing of experimental units), considering the mass of each tray. Weighings were carried out daily using a digital scale model 9094C/6 (Toledo do Brazil, São Bernardo do Campo, SP, Brazil), with an accuracy of 0.005kg, and water lost through evapotranspiration was replenished to maintain the defined water availability level.

The water availability of the tray was assessed based on the maximum water-holding capacity (WHC) of the SSB. Samples of the seed bank were collected before the start of the experiment (control sample). The control sample was saturated with water, and after free drainage, it was weighed to characterize the saturated weight. Subsequently, the control sample was placed in a forced air oven at 105°C for 24h to determine its dry weight. From this, the WHC value was calculated using the equation:

$$\mathrm{WHC} = P_{vs} - P_v - \left(\left(P_{sv} \times P_{as}\right) / P_a\right),$$

where P_{vs} = weight of the tray with saturated SSB (g); P_v = weight of the empty tray (g); P_{sv} = weight of the SSB in the tray (g); P_{as} = weight of the dry control sample (g); P_a = weight of the saturated control sample (g).

2.5 | Functional traits

For all individuals, four functional traits were measured: leaf area (m^2), stalk dry mass (g), leaf dry mass (g), and root dry mass (g). The leaf area for each scenario established in this study was determined using a LI-3100 leaf area meter (Li-Cor, USA).

To determine the stalk, leaf, and root dry mass production for each treatment, plant material from each individual was sectioned and separately placed in paper bags for a forced air oven at 65°C until reaching constant mass. Roots were washed to remove excess soil. After drying, the dry mass of each individual was weighed on a digital analytical balance with a precision of 0.0001g. These analyses were conducted at the end of the fifth month, which was the total period of emergence for all plants in the trays, including those that were transplanted.

2.6 | Vegetation sampling

The seedling emergence method (Brown, 1992) was adopted to conduct the seed bank evaluations during the 5months of experimentation. Individuals were identified by comparison with didactic collections from studies on natural regeneration and seed banks from projects developed at the Center for Scientific and Technological Research in Environment, Silviculture, and Ecology (NUPEMASE). Additionally, illustrated guides of seedlings and saplings published in Brazil (e.g., Viani, 2007), virtual herbaria such as JABOT (jabot.jbrj.gov.br) and Reflora (reflora.jbrj.gov.br), and the physical collection of the CAP herbarium, which contains voucher specimens registered in seasonal forests of the southern region of Espírito Santo, were used. Due to the inherent difficulty in identifying juvenile materials, because seedlings exhibit successive morphological differentiations,

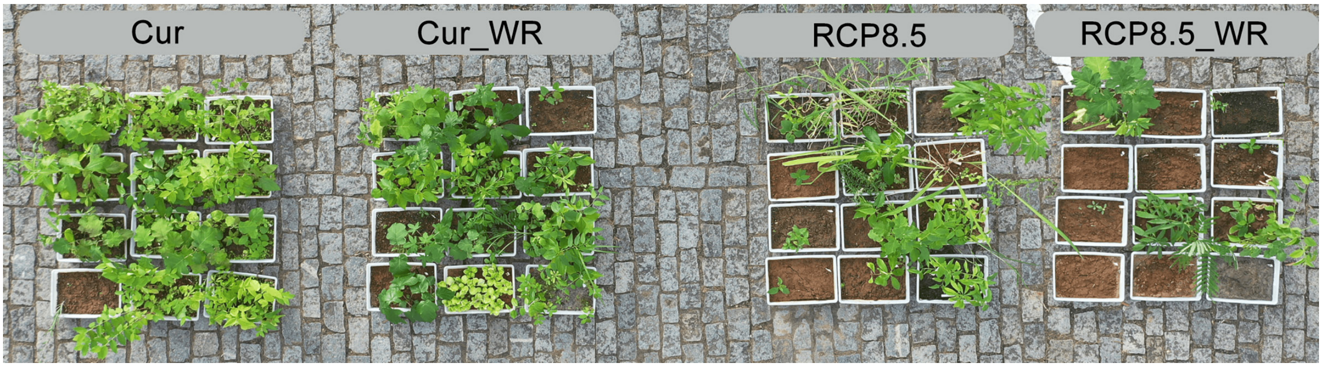

FIGURE 4 Emergency in the studied environments of the soil seed bank after 155 days. Semideciduous Seasonal Forest, in Pacotuba National Forest, ES, Brazil. Cur, current scenario without water restriction; Cur_WR, current scenario with water restriction; RCP8.5, future scenario without water restriction; RCP8.5_WR, future scenario with water restriction.

some specimens remained indeterminate. The families of angiosperms were classified using the APG IV system (APG IV, 2016), and species names, synonyms, and authorships were checked primarily on the Flora and Funga of Brazil list platform (www.reflora.jbrj.gov.br—see BFG, 2022) and additionally in the Missouri Botanical Garden database (tropicos.org).

The identified and properly analyzed individuals were removed from the trays to promote the emergence of other seeds and prevent contamination of the samples with propagules produced by the germinated plants. Those that were not identified but reached a high level of development or occasionally the reproductive stage were also removed from the trays and transplanted into polyethylene tubes with holes for water drainage for subsequent identification.

2.7 | Data analyses

The structural parameters (abundance and frequency), used for the structural description of the community, were calculated according to Mueller-Dombois and Ellenberg (1974) for the seed bank of each scenario studied using R software version 3.2.2 (R Core Team, 2023). To estimate the diversity and evenness of species in each scenario, Shannon, Simpson, and Pielou's evenness indices (Magurran, 2013) were calculated using the "vegan" package (Oksanen et al., 2019).

Species richness in the four sampled environments was evaluated in relation to the number of individuals and sample units using individual rarefaction and extrapolation curves with the "iNEXT" package (Hsieh et al., 2016). Richness was constructed using the first Hill number (species richness, $q=0$) (Chao et al., 2014). Extrapolations were made from abundance data, considering between two and three times the total sample size per environment type (Colwell et al., 2012). Rarefaction was estimated as the mean of 100 replicated bootstrap executions to estimate 95% confidence intervals. Whenever the 95% confidence intervals did not overlap, the number of species differed significantly at $p<.05$ (Colwell et al., 2012).

A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was run to test for differences in the taxonomic composition of the seed bank between the scenarios (factor with four levels). The significance was obtained using the function "adonis2" from the "vegan" package (Oksanen et al., 2019). To test for the homogeneity of variances between the scenarios, we performed permutational analysis of multivariate Dispersions (PERMDISP; Anderson et al., 2006). We used the function "betadisper" also from the "vegan" package (Oksanen et al., 2019). A principal coordinate analysis was used to visualize the results in a biplot, based on a distance matrix of Bray–Curtis.

The data were tested to check if they met the assumptions of residual normality and variance homogeneity. Since the data did not meet the assumptions of residual normality (Shapiro–Wilk test) and variance homogeneity (Levene's homoscedasticity test), the variable was subjected to the non-parametric Kruskal–Wallis multiple comparisons test ($p<.05$) to detect significant differences between the treatments. This analysis, along with the preliminary tests of normality and homoscedasticity, was conducted using the "stats" package. All analyses described in this section were carried out in R software version 4.3.0 (R Core Team, 2023).

3 | RESULTS

3.1 | Temperature and water

The average soil surface temperature throughout the day in the four treatments showed minimums around 6 a.m. (Cur: 19.4°C; Cur_WR: 19.2°C; RCP8.5: 21°C; and RCP8.5_WR: 21.8°C) and maximums around 12 p.m. (Cur: 28.8°C; Cur_WR: 29.8°C; RCP8.5: 32.6°C; and RCP8.5_WR: 37.5°C) (Figure 3c). Higher temperatures were observed in the treatments of the future scenario, especially in the treatment with water restriction. Within the SSB, at a depth of 2 cm, the temperature correlates with the surface temperature (Figure 3d). The coolest temperatures were found at 5 a.m. (Cur: 21.3°C; Cur_WR: 21.4°C; RCP8.5: 22.5°C; and RCP8.5_WR: 23°C), while the highest temperatures were at 12 p.m. (Cur: 29.5°C; Cur_WR: 29.9°C; RCP8.5: 34°C; and RCP8.5_WR: 35.4°C). With higher temperatures in the future scenarios, the total water consumption throughout the experiment was greater in the RCP8.5 (283.4 mm) and RCP8.5_WR (221.1 mm) treatments, followed by the Cur (106.5 mm) and Cur_WR (80.9 mm) environments (Figure 3e).

3.2 | Plant communities' structure

The total number of germinated propagules was 841 (density of 280 seeds m^{-2}) (Figure 4; Table 2). The number of individuals in the future scenarios was at least 70% lower than in the Cur scenario, with seed density and species richness following the same pattern of decline across the Cur_WR, RCP8.5, and RCP8.5_WR scenarios (Table 2). All individuals are distributed across 34 botanical families and 75 genera. At these taxonomic levels, there are 89 species, 21 morphotypes identified at the genus level, eight morphotypes at the family level, and 23 undetermined morphotypes (Table S1). For the total remnant, the Simpson diversity index (*C*) was 0.79, and the Pielou evenness index (*J*′) was 0.57. The current scenario without water restriction presented the highest number of exclusive species (24 species), followed by the current scenario with water restriction (22), and subsequently by the future scenarios without (16) and with water restriction (6) (Figure 5). In total, the four scenarios shared only six species: *Trema micrantha*, *Solanunm cordifolium*, *Solanum asperum*, *Muntingia calabura*, *Gamochaeta americana*, and *Cecropia glaziovii*.

Considering all treatments, the botanical families that stood out in terms of richness (species and morphotypes) were Asteraceae (13 spp.), Solanaceae (8), Cyperaceae (3), Euphorbiaceae (3), and Poaceae (3) (Table S1). Together, these families account for about 45% of all identified species and morphospecies. All other families were represented by only one or two species each. In the Cur environment, the families with the highest richness were Asteraceae (6 spp.), Solanaceae (5), and Urticaceae (2) (Table S1). In Cur_WR, the families were Asteraceae and Solanaceae with five species, and Apocynaceae, Euphorbiaceae, Piperaceae, and Urticaceae, each with two species. In RCP8.5, Asteraceae (5 spp.), Solanaceae (3), and Poaceae (2) stood out (Table S1). Finally, in the RCP8.5_WR environment, the Fabaceae and Solanaceae families presented two species each (Table S1).

TABLE 2 Floristic results and diversity indices (Shannon, Simpson, and Pielou) obtained in the studied scenarios. Semideciduous seasonal forest, Floresta Nacional de Pacotuba, ES, Brazil.

	Cur	Cur_WR	RCP8.5	RCP8.5_WR
Number of individuals	371	335	105	31
Seed density (m^2)	494	446	140	41
Total families	21	19	23	11
Total species	42	39	32	14
Shannon diversity (nats ind^{-1})	1.95	2.42	2.78	2.21
Simpson diversity index (*C*)	0.66	0.81	0.90	0.83
Pielou evenness index (*J*')	0.52	0.66	0.80	0.83

Abbreviations: Cur, current scenario without water restriction; Cur_WR, current scenario with water restriction; RCP8.5, future scenario without water restriction; RCP8.5_WR, future scenario with water restriction.

The highest abundance of individuals for the entire sampling effort was obtained by the family Muntingiaceae (364 individuals), followed by Solanaceae (99), Piperaceae (56), Urticaceae (52), Melastomataceae (46), and Euphorbiaceae (44). The most abundant family was represented by only one species, considered exotic and with invasion potential, *Muntingia calabura* L., which emerged in all studied environments (Table S1). In terms of genera, only seven had two or more species: *Solanum* (6 species), *Piper* (2 species), *Cecropia* (2 species), *Mikania* (4 species, each with a single occurrence), *Cyperus* (3 species, each with one occurrence), and *Leonurus* and *Ipomoea* (each with two species with a single occurrence).

The species with the highest abundance were *M. calabura* (364 individuals), *Solanum asperum* Rich (68), *Piper* cf. *amplum* Kunth (46), *Cecropia glaziovii* Snethl. (43), and *Tovomitopsis paniculata* (Spreng.) Planch. & Triana (41), which together represent approximately 67% of the individuals. Regarding the studied environments, *M. calabura* was more abundant in the current scenario (Cur: 211 and Cur_WR: 133), while in the future scenario (RCP8.5: 16 and RCP8.5_WR: 11), it was *S. asperum*. Both were sampled in all areas and are the two most abundant species, indicating a high proliferation of seeds from these species (zoochory). The other species that appeared in all studied environments were *Gamochaeta americana* (Mill.) Wedd, *Trema micrantha* (L.) Blume, *Solanum cordifolium* Dunal, and *Cecropia glaziovii* Snethl. Species that presented only one individual represent 67% of the identified species and morphotypes (Table S1).

The non-parametric Kruskal–Wallis test revealed significant differences among the studied treatments in terms of abundance (Figure 6). The Cur scenario showed the highest values, differing from the density of the RCP8.5 and RCP8.5_WR environments and did not statistically differ from Cur_WR. Cur_WR statistically differed from the future treatments. The environments in the future scenario were significantly different from each other, with RCP8.5_WR being the treatment with the lowest value.

A significant difference was found in the taxonomic composition of the four scenarios for seed bank (PERMANOVA: $F = 3, 8203$, df = 3; $p = .001$). The results of PERMDISP analysis showed no significant difference ($F = 1, 3482$, df = 3; $p = .2728$) in the homogeneity of variance of the species composition between scenarios (Figure 7).

The Cur and Cur_WR treatments showed the highest species richness for the number of sample units and individuals (Figure S1a,b). Similar richness was observed between the Cur and Cur_WR treatments and between Cur_WR and RCP8.5 using rarefaction and extrapolation curves based on sample units (Figure S1a). However,

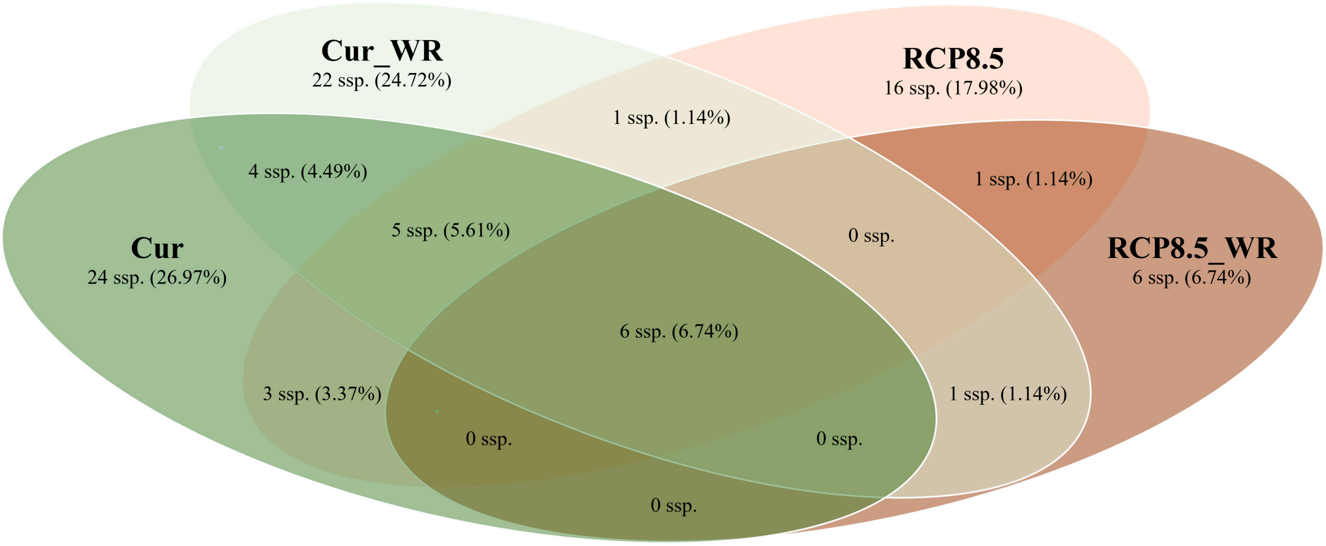

FIGURE 5 Species sharing in the soil seed bank across the environments studied by Venn diagram in a remnant of seasonal semideciduous forest, at Pacotuba National Forest, ES, Brazil. Cur, current scenario without water restriction; Cur WR, current scenario with water restriction; RCP8.5, future scenario without water restriction; RCP8.5 WR, future scenario with water restriction.

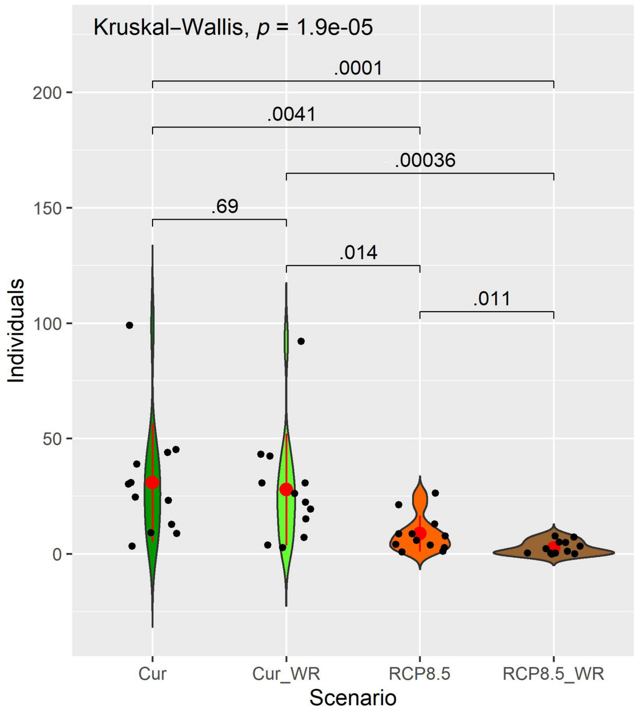

FIGURE 6 Nonparametric Kruskal–Wallis test ($p < .05$) comparing the abundance of the four studied environments (Cur, Cur_WR, RCP8.5, and RCP8.5_WR) in a semideciduous seasonal forest remnant, the Pacotuba National Forest, ES, Brazil. Cur, current scenario without water restriction; Cur_WR, current scenario with water restriction; RCP8.5, future scenario without water restriction; RCP8.5_WR, future scenario with water restriction.

there are differences between Cur and Cur_WR and RCP8.5 in terms of the number of individuals (Figure S1b), with RCP8.5_WR showing lower species richness (Figure S1b).

3.3 | Leaf area and dry mass production

The total leaf area sum showed significant differences among the treatments by the non-parametric Kruskal–Wallis test (Figure 8a). The RCP8.5_WR scenario, which had the lowest total leaf area sum (1.85 m^2), differed statistically from the other treatments (Figure 8a). The Cur, Cur_WR, and RCP8.5 treatments did not show significant differences among them.

The non-parametric Kruskal–Wallis test revealed significant differences among the treatments studied regarding the dry mass of leaves, stalks, and total dry mass of individuals (Figure 8). The test did not show significant differences among treatments for root dry mass. The RCP8.5_WR environment differed statistically from the other environments for leaf dry mass (Figure 8b), stalk dry mass (Figure 8c), and total dry mass (Figure 8d). There were no significant differences among the other treatments studied.

4 | DISCUSSION

The results showed that climate change, a conditioning factor of environmental changes, influences the composition, abundance, diversity, and assessed functional traits of plant species in the SSB of semideciduous seasonal forests. Due to the lack of data describing how seedlings of these seasonal vegetations will respond to climate change, this study provides the first experimental-based information, in a simulated environment, on the emergency of plant species present in the SSB under current and future climates. This information is essential for understanding processes that threaten ecosystem resilience, affect species distribution, and may favor biological invasion by exotic plants and/or those with invasive potential.

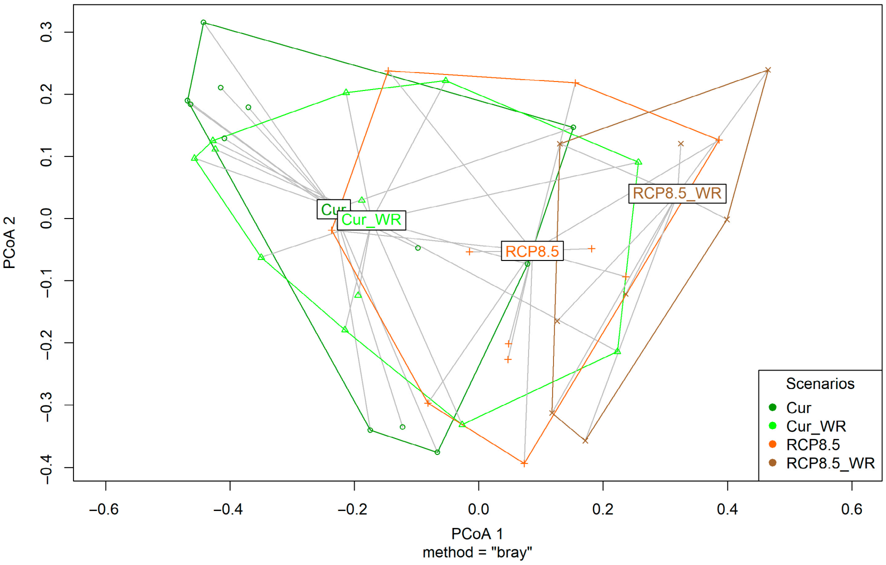

FIGURE 7 Principal coordinates analysis (PCoA) based on species composition among trays from the four studied scenarios (Cur, Cur_WR, RCP8.5, and RCP8.5_WR), using Bray–Curtis distance. Semideciduous seasonal forest, at Pacotuba National Forest, ES, Brazil. Cur, current scenario without water restriction; Cur WR, current scenario with water restriction; RCP8.5, future scenario without water restriction; RCP8.5 WR, future scenario with water restriction.

4.1 | Temperature and water

Differences between surface and subsurface temperatures and water restriction strongly influenced seed emergency in the seasonal forest, reducing all assessed composition and structure parameters in the pessimistic scenario. Although soil temperature plays an important role in seedling emergence (Du et al., 2023; Gioria et al., 2020; Ooi, 2012; Ooi et al., 2009; Royer et al., 2011; Yang et al., 2021), temperatures higher than the optimal plant growth limits (Enríquez-de-Salamanca, 2022; Silva, Calvi, et al., 2021) increase seed mortality rates, transpiration of newly formed leaves, and reduce the proportion of viable seeds in the soil (Enríquez-de-Salamanca, 2022; Ooi, 2012; Silva, Calvi, et al., 2021). These conditions can be even more critical for seasonal forests, where nearly half of the trees are deciduous during the driest months of the year, increasing the amount of sunlight reaching the forest floor and increasing temperature and evapotranspiration, as we verified in the future scenario, where the temperature increase required approximately twice as much water as in the current scenario.

Water restriction, in turn, maybe the most critical variable for seed emergency and seedling establishment in vegetation. In the Caatinga domain, a dry tropical forest, some specialized species did not have emergency inhibited at high temperatures, but annual precipitation below expectations was critical for the emergency of these species (Dantas et al., 2020). In the same context, in a future scenario with water scarcity, the seed bank of the seasonal forests (less dry) will be dangerously vulnerable, increasing the risk of local extinction of species over time (Venable, 2007). Furthermore, in the future scenario (RCP8.5_WR), seed abundance, richness, and density decreased dramatically and the number of species exclusive to each treatment was high (Figure 5), showing that many species are intolerant to these climatic conditions of severe water limitation (Gonzalez & Ghermandi, 2021), affecting the resilience of the forest seed bank and progressively the structure of these ecosystems.

4.2 | Plant communities' structure

Some of the global consequences of climate change already confirmed include loss of diversity and alteration in the structure, demography, and distribution of species in tropical forests (e.g., Artaxo et al., 2022; Deb et al., 2018; Yang et al., 2021). In seasonal forests, although evolutionary evidence suggests the persistence of species adapted to climatic seasonality, those still intolerant to this condition may be vulnerable in the future (Calvo-Rodriguez et al., 2021; Pennington et al., 2009; Petrie et al., 2017). With high temperatures and water deficit, the emergency of many species is inhibited, as observed with *Schizolobium parahyba*, a species whose growth is determined by precipitation in the driest season of the year (Latorraca et al., 2015).

Most of the species found are characteristic of early succession and with rapid growth. Water restriction negatively impacts the demographics of these species by increasing mortality and reducing recruitment rates (Song et al., 2023; Walck et al., 2011). Additionally, mechanisms involving resource allocation, such as xylem hydraulic conductivity, make fast-growing species more vulnerable to water stress (Song et al., 2023).

In dry tropical forests (Dantas et al., 2020) and arid ecosystems (Kumarathunge et al., 2020; Lewandrowski et al., 2021), the responses of seeds and seedlings to climate change and water stress have been critical in terms of viability, germination, and establishment, following the trend found in our study. Prolonged water limitation reduces seed viability, germination, and seedling establishment, and consequently, lowers recruitment.

Muntingia calabura, the most abundant species in the seed bank, is an exotic plant and native to Central America and was first described in a dry tropical forest in Costa Rica (Fleming et al., 1985; Muhammad Ansori et al., 2021). In Brazil, it is not included in the list of invasive exotic species by the Hórus Institute (https://bd.institutohorus.org.br/); however, it is a species with limited available information and needs an evaluation of its possible invasive potential.

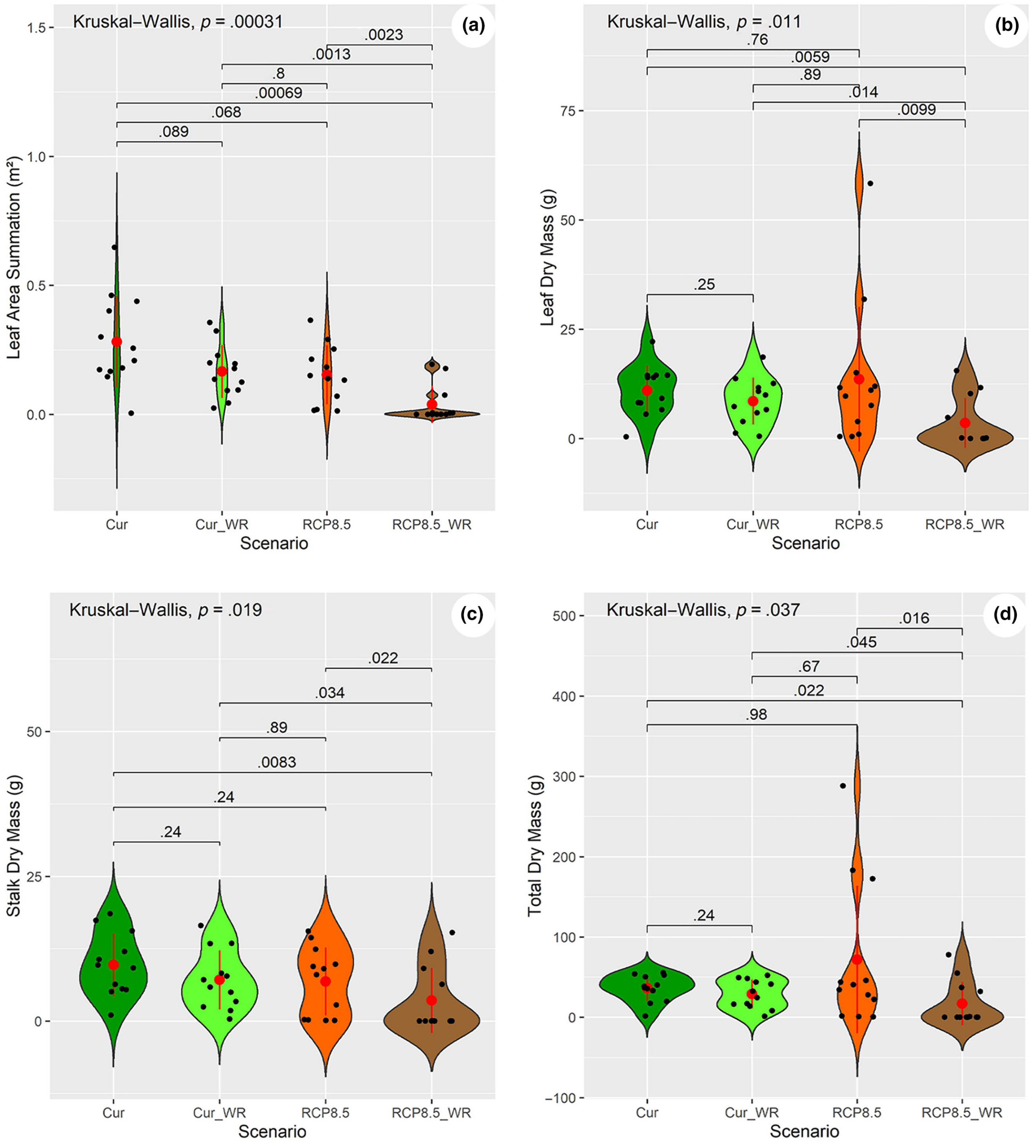

FIGURE 8 Nonparametric Kruskal–Wallis test ($p < .05$) of the total leaf area sum (m^2) (a), dry mass of leaves (b), stalks (c), and total dry mass (d) of individuals in the four studied environments (Cur, Cur_WR, RCP8.5, and RCP8.5_WR) from a semideciduous seasonal forest, in Pacotuba National Forest, ES, Brazil. Cur, current scenario without water restriction; Cur WR, current scenario with water restriction; RCP8.5, future scenario without water restriction; RCP8.5 WR, future scenario with water restriction.

As in our study, *M. calabura* was also abundant in the seed bank of another conservation unit in a seasonal forest (Silva, Martins, et al., 2021), reinforcing the need to assess the risk of invasion, especially in semideciduous forests, and the consequent impact on the structure of these ecosystems.

Summarizing, once the drastic change in floristic composition, abundance, and diversity due to experimentally induced climate change is detected, even if adult plants tolerate such adverse conditions, seed regeneration will be severely impaired by water restriction. Thus, the percentage of woody species will decrease in terms of emergency and seedling survival in the worst-case scenario studied, increasing mortality, reducing recruitment, and altering forest structure and dynamics.

4.3 | Leaf area and dry mass production

Forests in drier environments attain lower basal area and leaf area index than forests in wetter locations (McDowell & Allen, 2015). Drought strongly alters root morphological characteristics, increasing their mortality rate (Zhou et al., 2018). Thus, low soil water levels can inhibit their absorption by roots and decrease sap flow, compromising plant growth and development (Taiz et al., 2017). These findings help to explain the low values found for the most pessimistic scenario for the seasonal forest (RCP8.5_WR). In addition, the low number of individuals emerging in this scenario may be even below their maximum productivity and biomass, and show adaptations to water stress, such as changes in growth rates and reduced leaf area (Carter & White, 2009).

In general, we found a significant downward trend in functional traits between climate scenarios (Figure 8). These results are explained by a primary adaptive trait of plants to water deficit and high VPD, namely the reduction of leaf area due to increased accumulation of structural carbohydrates (Taiz et al., 2017; Trugman et al., 2019) (Figure 8a). In addition, low specific leaf area promotes greater efficiency in the uptake of the limiting resource, carbon, required for proper growth (Bloom et al., 1985). In this context, a decrease in productivity and biomass and an increase in seedling mortality are expected under climatic conditions of increasing drought periods and a warming atmosphere, driven by rising atmospheric CO_2 levels (Becknell et al., 2012; McDowell et al., 2022).

4.4 | Acting now

Climate change and prolonged water restriction could drastically alter the structure of seasonal forests in the future by causing a loss of seed viability, increased seed and seedling mortality, and reduced recruitment of new individuals. Protected areas, like our study site, will be impacted and will require new conservation protocols and policies. In this case, activities such as collecting and storing seeds in germplasm banks and planting species that are tolerant to prolonged droughts may be alternatives to protect diversity both in situ and ex situ. *At the same time*, long-term strategies are developed and implemented.

Immediate actions to mitigate the effects of climate change (for the present) are also fundamental tasks, often based on the absorption of atmospheric carbon through tree planting, considering the maintenance of non-forest natural systems and the implementation of agroforestry systems (Tölgyesi et al., 2022; Zomer et al., 2022). Additionally, identifying priority areas for the conservation of threatened species in seasonal forests (e.g., Menezes et al., 2021) and proper, consistent planning for the control of exotic species with high expansion capacity in future climates (e.g., Fulgêncio-Lima et al., 2021) are procedures that should be included in conservation policies for these forests.

Thus, our findings serve as another warning to authorities and decision makers to mitigate the causes of climate change such as deforestation, forest fires, and the predominantly fossil energy matrix. Since the United Nations Climate Change Conferences through the Conference of the Parties, authorities from hundreds of countries have committed to fulfilling the signed agreements and protocols, yet the implemented actions have not been sufficient. Meanwhile, climate change denial movements are growing worldwide, often fueled by political authorities (Shue, 2023), which hinder fundamental agendas to reduce the effects of climate change.

AUTHOR CONTRIBUTIONS

Patrícia Borges Dias: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing – original draft. **Sustanis Horn Kunz:** Conceptualization; methodology; project administration; supervision. **José Eduardo Macedo Pezzopane:** Conceptualization; funding acquisition; methodology; supervision. **Talita Miranda Teixeira Xavier:** Conceptualization; data curation; funding acquisition; methodology; validation. **João Paulo Fernandes Zorzanelli:** Conceptualization; data curation; methodology; validation. **João Vitor Toledo:** Conceptualization; data curation; formal analysis; software. **Lhoraynne Pereira Gomes:** Data curation; formal analysis; software; validation. **Rodrigo Gomes Gorsani:** Data curation; formal analysis; software; validation.

ACKNOWLEDGMENTS

This study was partially financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brazil (CAPES) and the Fundação de Amparo à Pesquisa e Inovação do Espírito Santo (FAPES). This study was also supported by the National Council for Scientific and Technological Development (CNPq, Programa de Capacitação Institucional—PCI/INMA) of the Brazilian Ministry of Science, Technology and Innovation (MCTI).

CONFLICT OF INTEREST STATEMENT

There is no conflict of interest in this section of the article.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/rn8pk0pmn.

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How to cite this article: Dias, P. B., Horn Kunz, S., Pezzopane, J. E. M., Xavier, T. M. T., Zorzanelli, J. P. F., Toledo, J. V., Gomes, L. P., & Gorsani, R. G. (2024). Water restriction alters seed bank traits and ecology in Atlantic Forest seasonal forests under climate change. *Global Change Biology*, *30*, e17494. https://doi.org/10.1111/gcb.17494